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Icelopagurus tuberculosus, a distinct new hermit crab species (Crustacea: Decapoda: Paguridae) from Japan

Akira Asakura

Natural History Museum and Institute, Chiba, 955-2, Aoba-cho, Chuo-ku, Chiba 260-8682, Japan

Abstract.—A new species of pagurid hermit crab of the genus *Icelopagurus* McLaughlin, *I. tuberculosus*, is described and illustrated. It is the second species in the genus and is distinct in having a large well-calcified, immovable plate that is partially fused with the shield's posterior and posterolateral margins, a transverse row of four prominent protuberances on the dorsal surface of the shield, a pair of similar protuberances on each anterolateral margin of the shield, and a somewhat reduced abdomen. The new species is compared with the only other congeneric species, *I. crosnieri* McLaughlin. Morphological similarities and differences of *Icelopagurus* with selected, specialized pagurid genera are discussed.

In the course of studies of the decapod crustacean fauna from the Ryukyu Archipelago (Okinawa) by Keiichi Nomura of the Kushimoto Marine Park and his coworkers, numerous specimens of hermit crabs were collected and given to the author for identification. A partial account of these hermit crabs was published together with data on other decapod crustaceans (Nomura et al. 1996). However, a number of specimens still remained unidentified, some of which resemble species of *Catapagurus* A. Milne Edwards, 1880 with sabre blade-like dactyls on the ambulatory legs, although the males differ in having a short sexual tube.

McLaughlin (1997) recently established the monotypic genus *Icelopagurus* for *I. crosnieri* McLaughlin, 1994, based on specimens collected from Indonesian waters. *Icelopagurus* is superficially similar to *Catapagurus* but differs in the shortness of the sexual tube in males, which does not curve up over the dorsal surface of the body, and by the distinct development of the telson. The specimens from the Ryukyu Archipelago belong to *Icelopagurus* and represent a new species described herein.

Material and Methods

Collections were made by SCUBA diving on coral reefs of the Kumejima Island, northern part of the Ryukyu Archipelago (Okinawa), Japan. Specimens were fixed in 10% formalin solution and then transferred to 75% alcohol solution for preservation. Specimens were stained with a 5% Methylene Blue solution and examined under a stereoscopic microscope OLYMPUS SZH and using a NIKON UW for high magnification. Drawings were made using a camera lucida attachment. All specimens are deposited in the Natural History Museum and Institute, Chiba, with the registration code CBM-ZC.

Terms used in this study follow McLaughlin (1974) in general, and Lemaitre (1995) for the cephalothorax.

Shield length (SL), measured from the tip of the rostrum to posterior end, is used as indicator of size. The length of segments in chelipeds and cephalic appendages is measured along the dorsomedian line. The length of segments in the second and third pereopods is measured along the lateromedian line.

To evaluate the affinities of the new species, material of the following species was examined: *Icelopagurus crosnieri*, paratypes, 1 ♀, SL = 3.15 mm, 1 ov. ♀, SL = 3.90 mm, 884–891 m, Station CP91, 8°44′S–131°05′E, Tanimbar Islands, Indonesia, 5 Nov 1991, Karubar Cruise, Muséum national d'Histoire naturelle, Paris, MNHN-Pg 5279; *Catapagurus ensifer* Henderson, 1893, syntypes, 2 ♂, SL = 2.40, 2.35 mm, 1 ♀, SL = 2.40 mm, 2 ov. ♀, SL = 2.15, 2.45 mm, Gulf of Martabian, Burma, The Natural History Museum, London, 1888.34; *Catapagurus granulatus* Edmondson, 1951, holotype, ♂, SL = 2.58 mm, 58–79 m, off Bird Island, Hawaii, Bernice P. Bishop Museum, Hawaii, BPBM 5446, paratypes, 2 ♂, SL = 2.05, 2.00 mm, 36–49 m, off the south coast of Oahu, Hawaii, BPBM No. 5514; *Catapagurus japonicus* Yokoya, 1933, syntypes, 3 ♂, SL = 2.10, 2.60, 2.95 mm, st. 324, Bungo Strait, 106 m, 21 Jul 1928, Kitakyushu Museum of Natural History; 1 ♂, SL = 2.20 mm, 65 m, Maruyamadashi, Amadaiba, Sagami Bay, 27 Jul 1958, Biological Laboratory, Imperial Household, Showa Memorial Institute, Tsukuba, BLIH 1474; 1 ♂, SL = 2.65 mm, 84–85 m, Aoyamadashi-Maruyamadashi, Amadaiba, Sagami Bay, 24 Jan 1968, BLIH 3551; 1 ovi. ♀, SL = 3.10 mm, 80–85 m, 2.41 km western southwest off Jyougashima Island, Sagami Bay, 25 Jul 1959, BLIH 1615.

Icelopagurus tuberculosus, new species

Figs. 1A–H, K–M, 2–4

Holotype.—♂, SL = 5.70 mm, CBM ZC 4700, outer side of coral reefs, northern coast of Kumejima (26°20′N, 126°45′E), Shimajiri-gun, Okinawa-ken, Ryukyu Archipelago, SCUBA diving, coll. Yuisho Sakamoto, 16 Aug 1993.

Paratypes.—1 ♂, SL = 4.90 mm, CBM ZC 4701; 1 ♀, SL = 5.10 mm, CBM ZC 4702; same data as holotype.

Type locality.—Kumejima, Ryukyu Archipelago.

Description.—Eleven pairs of phyllobranchiate gills: 2 pairs of arthrobranchiae on either side of coxo-thoracic articulations of third maxilliped and first to fourth pereopods, plus 1 pair of pleurobranchiae on either side of pleural plate of seventh thoracic somite (above fourth pereopod).

Shield (Fig. 1A, B, D) slightly broader than long, 1.12:1.00; anterior margin between rostrum and lateral projections distinctly concave and terraced; anterolateral margins each bearing prominent protuberance armed with numerous often spiniform tubercles on middle portion; lateral margins straight and armed with numerous spiniform tubercles; posterolateral margins irregular; posterior margin truncate. Dorsal surface of shield vaulted and rugose, covered with numerous often spiniform tubercles and scattered with short setae; anterior region with a transverse row of 4 prominent protuberances armed with numerous often spiniform tubercles; posterolateral regions each with 3 distinct incisions. Rostrum broadly rounded, overreached by lateral projections. Lateral projections distinctly produced, triangular, upturned. Anterior faces of shield between rostrum and lateral projections each with 3–5 distinct blunt-tipped spines on ventral margin laterally. Very broad, flat, well-calcified plate surrounding margin of posterior half of shield (Fig. 1A), unarmed, with scattered long setae; partially fused with shield, immovable; lateral and posterior margins straight and edged.

Posterior carapace (Fig. 1A, B) with pair of partially calcified broad bands in areas between cardiac sulci and sulci cardiobranchialis, broader anteriorly; partially calcified, small plate present between cardiac sulci, abutting to medial portion of posterior margin of accessory portion of shield; linea anomurica extending from anterior extremity of accessory portion of shield to subproximal portion of ventrolateral margin of posterior carapace. Branchiostegites (Fig. 1B) not calcified except for somewhat calcified anterodorsal margin; anterodorsal and anterior margins unarmed.

Ocular peduncles (Fig. 1A, D) short, distinctly shorter than shield, 0.30:1.00; each with constriction near base of cornea; strongly tuberculate dorsally and dorsomesially; corneae dilated; basal margins of corneae each fringed with thick, long setae dorsally and mesially. Ocular acicles distinctly shorter than ocular peduncles, 0.40: 1.00; elongated triangular, subacute; separated basally by width of rostrum; mesial margins fringed with few, thick setae; lateral margins with few short, fine setae. Interocular plate rectangular, calcified; separated from surrounding region by soft membrane.

Antennular peduncles (Fig. 1A, E, F) very long, with penultimate segment exceeding ocular peduncle (excluding cornea) by approximately 0.80 own length, when fully extended. Ultimate segment unarmed, with few long setae dorsodistally. Penultimate segment unarmed, with few short setae on dorsal face subdistally. Basal segment slightly produced distomesially, with 1 acute spinule at ventrodistal mesial angle.

Antennal peduncles (Fig. 1A, B, G, H) moderately long, with distal margin of fourth segment reaching beyond base of corneae but not to distal margin, when fully extended; with supernumerary segmentation. Fifth and fourth segments with few scattered long setae. Third segment with ventrodistal angle produced. Second segment with dorsolateral distal angle produced, terminating in strong spine accompanied ventrally by short accessory spine, dorsolateral face with several tubercles, dorsomesial distal angle with acute spine. First segment with strong, hook–shaped spine laterally and strong spine at ventrodistal margin mesially. Antennal acicle moderately short, overreaching ocular peduncles; straight, blunt-tipped, with scattered setae; mesial face slightly tuberculate. Flagella very long, 6.2 times length of shield, scarcely setose.

Mandible (Fig. 2A) without distinguishing characters. Maxillule (Fig. 2B, C) with external endopodal lobe obsolete; internal lobe with 1 apical bristle. Maxilla (Fig. 2D) with moderately broad scaphognathite. First and second maxillipeds (Fig. 2E, F) without distinguishing characters. Third maxilliped (Fig. 2G–1) with 3 acute corneous teeth on basis; ischium with crista dentata well developed, composed of 15–16 corneous teeth and with 1 strong accessory tooth; merus with acute dorsodistal spine.

Sternite of 3rd maxillipeds unarmed, with shallow median cleft.

Right cheliped of male (Fig. 3A–D) larger and stouter than that of left; compressed dorsoventrally. Dactyl distinctly shorter than palm, 0.32:1.00; forming weak hiatus with fixed finger; terminating in strong, curved calcareous claw; dorsal face convex, tuberculate mesially, with tufts of long setae; cutting edge with prominent blunt-tipped calcareous tooth medially. Fixed finger with dorsal surface tuberculate, with tufts of long setae; cutting edge with minute calcareous teeth on distal half. Palm very long, with dorsal surface covered with numerous spiniform tubercles, with 2 faint longitudinal sulci on proximal ⅔, continuing to proximal very deep depression, dorsomesial and dorsolateral surfaces covered with dense tubercles, with proximal angles protruded and strongly armed with spiniform tubercles; ventral surface covered with dense minute tubercles and scattered long setae. Carpus distinctly shorter than palm, 0.56:1.00; swollen distally; dorsal surface flat, with scattered spiniform tubercles, dorsolateral and dorsomesial margins forming distinct ridges, each armed with strong spiniform tubercles; lateral, mesial and ventral surfaces glabrous. Merus with dorsal margin irregular, covered with strong spiniform tubercles and protuberances, and scattered long setae, dorsodistal angle bearing slightly upturned large spine; lateral and mesial faces tuberculate, ventromesial and ventrolateral faces tuberculate with distal angles only protruded. Ischium with very strong, acute spine on ventrodistal margin laterally. Coxa with tubercles on ventromesial distal angle.

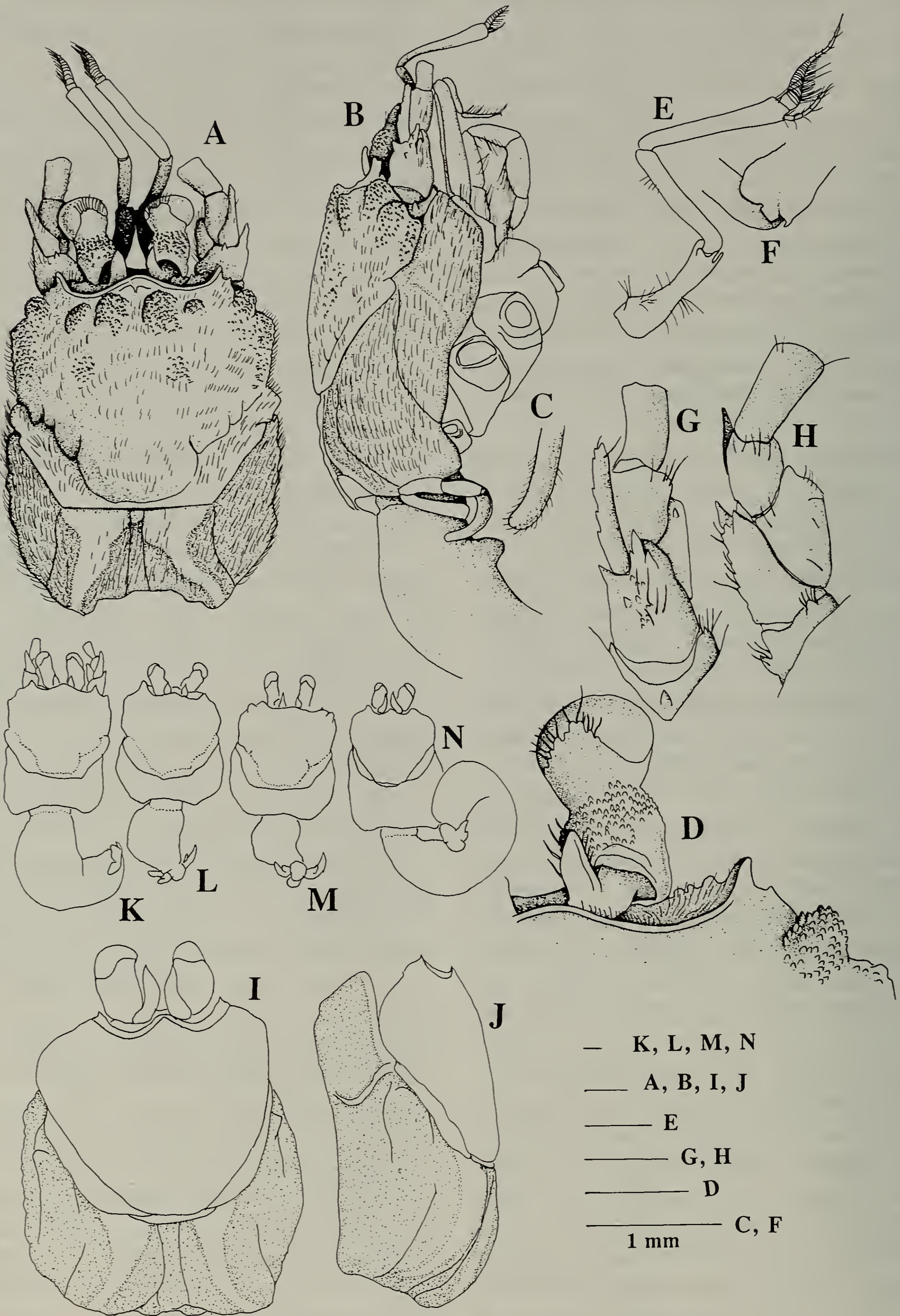

Fig. 1. *Icelopagurus tuberculosus*, new species: holotype male, SL = 5.70 mm, Okinawa, Japan (CBM ZC 4700); A–H, cephalothorax and cephalic appendages: A, whole (dorsal view); B, whole (right lateral view); C, tip of sexual tube arising from coxa of right fifth pereopod; D, ocular peduncle and anterolateral portion of shield (right, dorsal view); E, antennule (right, lateral view); F, same, distal portion of basal segment (mesial view); G, antenna (right, lateral view); H, same (ventral view); K–M, proportion of cephalothorax and abdomen: K, holotype male; L, paratype male, SL = 4.90 mm (CBM-ZC 4701); M, paratype female, SL = 5.10 mm (CBM-ZC 4702). *Icelopagurus crosnieri*

Left cheliped of male (Fig. 3E–G) slightly shorter than that of right, 0.92:1.00; considerably more slender than right, 0.65:1.00 in widest portion of palm and 0.32:1.00 in widest portion of carpus, respectively. Dactyl strongly curved distally, forming large hiatus with fixed finger; approximately equaling palm in length, with tufts of long setae; terminating in strong corneous claw; cutting edge with numerous tiny corneous teeth. Fixed finger tuberculate laterally, with tufts of long setae; terminating in strong recurved corneous claw; cutting edge with numerous tiny corneous teeth. Palm with dorsal surface tuberculate, with very broad faint longitudinal sulcus on proximal half continuing to proximal depression; mesial, lateral and ventral surfaces covered with dense blunt or spiniform tubercles. Carpus moderately long, approximately equaling palm in length; dorsal surface flat, with numerous blunt or spiniform tubercles, dorsolateral and dorsomesial margins distinct, each armed with strong, spiniform tubercles; mesial and lateral faces granular or tuberculate. Merus with dorsal margin strongly tuberculate, dorsodistal angle bearing very large spine; lateral face granular; ventrolateral margin tuberculate, with distal angle bearing blunt-tipped spine, ventromesial distal angle only produced and unarmed. Ischium with strong spine at ventrolateral distal angle.

Second (Fig. 2J–O) and third (Fig. 2P–R) pereopods morphologically similar; third slightly longer than second, 1.09:1.00, especially dactyl of third longer than second, 1.15:1.00, but broader in second than in third (ratio of width/length = 0.17 in second but 0.12 in third). Dactyls slightly shorter than propodi (second), 0.91:1.00, or as long as propodi (third); broad, sabre blade-shaped; each terminating in strong corneous claw; mesial faces concave longitudinally, with scattered long setae; dorsomesial and ventromesial margins each with row of corneous spinules; lateral faces slightly convex longitudinally. Propodi with entire surfaces minutely tuberculate; dorsal margins each with 2 to 5 thick, spine-like setae, dorsodistal margins each with pair of thick, spine-like setae; ventral margins each with 1 or 2 thick, spine–like setae. Carpi each with tiny spinule at dorsodistal angle; dorsal, lateral and mesial surfaces covered with dense tubercles or granules. Meri with dorsal, lateral and mesial surfaces tuberculate; dorsal face tuberculate, dorsodistal angles each only slightly protruded (second) (with tiny spinule on left second of paratype male) or bearing very strong spine (third); dorso-subdistal portion with 1 strong spine (second, but 2 spines in right second of paratype male), or 2 strong spines (third); ventrolateral distal angles each bearing large spine (second) or slightly protruded (third), ventromesial distal angles unarmed; distal half of ventrolateral margins slightly (second) or strongly (third) expanded ventrally, but ventromesial margins not. Female with coxae of third pereopods each with gonopore (Fig. 4N).

Fourth pereopods (Fig. 4A–C) semichelate. Dactyl moderately long, terminating in strong corneous claw; prominent preungual process present, covered with dense short setae; cutting edge with several corneous teeth. Propodus with rasp composed of 1 row of strong corneous scales along 0.80 length of ventral margin; dorsodistal angle unarmed. Carpus with blunt-tipped spine at dorsodistal angle.

Fifth pereopods chelate (Fig. 4D). Dactyls and propodi with well developed rasps. Male (Fig. 1B, C) with right coxa bearing moderately-short sexual tube directed to exterior; sexual tube with blunt-tipped apex, not filamentous, covered with scattered

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McLaughlin, 1997: paratype female, SL = 3.15 mm, Tanimbar Island, Indonesia (MNHN-Pg 5279): I, carapace, dorsal view; J, same, lateral view; N, proportion of cephalothorax and abdomen. Scales = 1 mm.

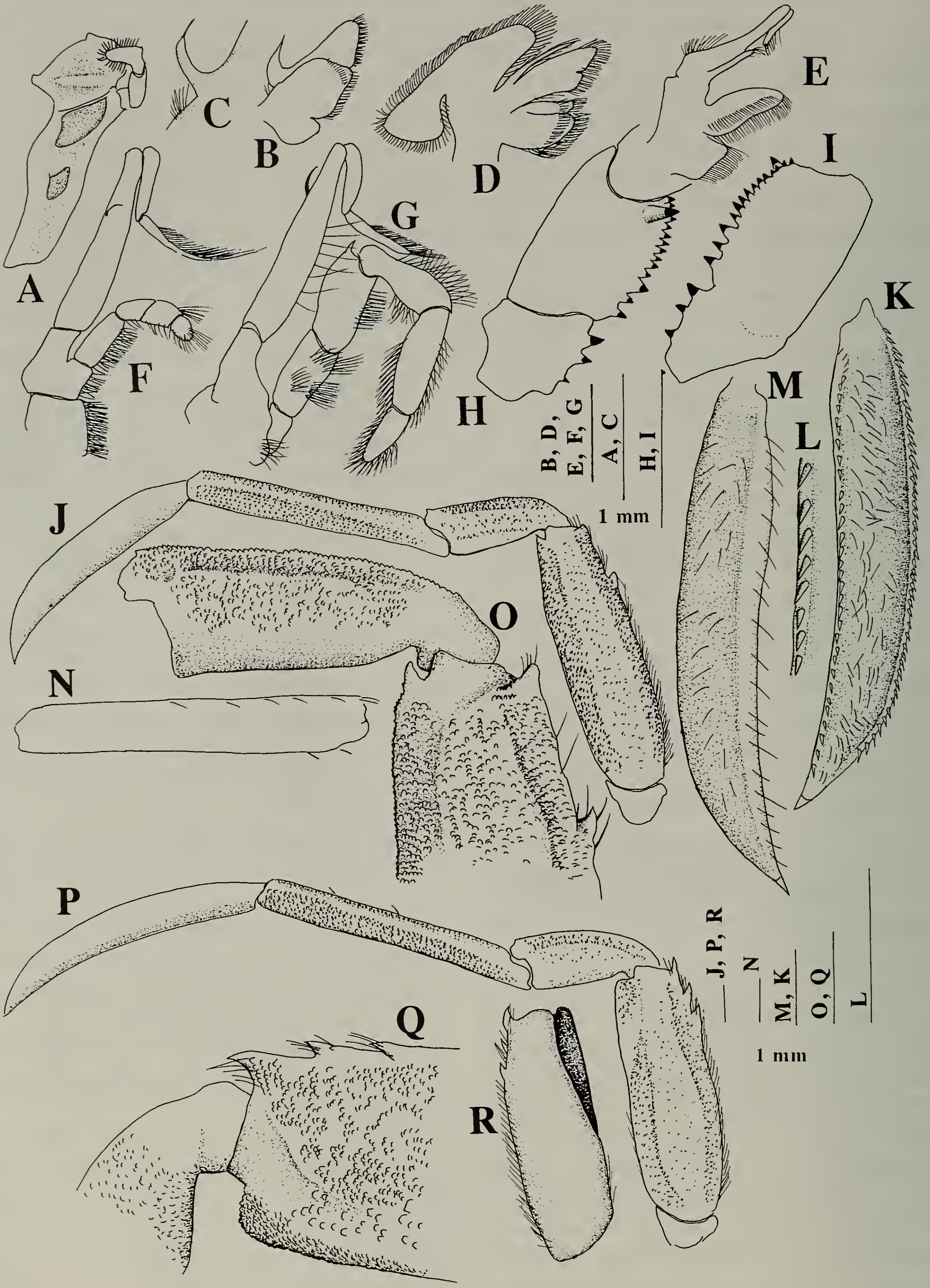

Fig. 2. *Icelopagurus tuberculosus*, new species: holotype male, SL = 5.70 mm, Okinawa, Japan (CBM ZC 4700); A–I, mouthparts (right): A, mandible (internal view); B, maxillule (external view); C, same, endopod; D, maxilla (external view); E, first maxilliped (external view); F, second maxilliped (external view); G, third maxilliped (external view); H, same, ischium and basis (external view); I, same, ischium and basis (internal view); J–O, second pereopod (left): J, whole (lateral view); K, dactyl (mesial view); L, same, ventral portion of mesial face; M, same (lateral view); N, propodus, schematic diagram indicating condition of spine-like setae

short setae apically; gonopore of left coxa (Fig. 4E) with vas deferens only slightly protruded, obscured by dense short setae posteriorly and dense medium-length setae anteriorly. Female with nearly symmetrical coxae (Fig. 4O).

Sternite of second pereopods (Fig. 4F) broad, subrectangular; divided into 2 lobes by longitudinal shallow median groove; anterior margin of each lobe round, unarmed, with long setae. Sternite of third pereopods (Fig. 4F, G) with perpendicular anterior lobe bearing pair of small projections armed with minute tubercles and fringed anteriorly with setae; horizontal posterior plate very broad, with setae anteriorly; subdivided into 2 lobes by longitudinal shallow median groove. Sternite of fourth pereopods (Fig. 4F) as transverse rod, accompanied by setae anteriorly. Sternite of fifth pereopods (Fig. 4E, F) reduced to very narrow transverse rod with pair of round projections with setae; widely separated from preceding sternal plates.

Abdomen (Fig. 1K–M) small in holotype male, comparatively reduced in paratype male, reduced in paratype female; membranous, dextrally twisted. Tergite of first abdominal somite small and chitinous. Tergites of second to fifth abdominal somites not clearly delineated, membranous. Tergite of sixth abdominal somite calcified, subrectangular, unarmed; divided into anterior and posterior lobes by shallow, transverse groove. Male with 3 unpaired left uniramous pleopods (Fig. 4H–J) fringed with long setae, arising from third to fifth abdominal somites. Female with no paired first pleopods modified as gonopods but with 3 unpaired left biramous pleopods (Fig. 4P–R) arising from second to fourth abdominal somites; existence of fourth pleopod uncertain because of damaged abdomen of single female specimen. Uropods (Fig. 4K, L) strongly asymmetrical, left distinctly larger than right; rasps of exopods and endopods well developed; protopods with some tubercles on posterodistal face (right) or unarmed (left). Telson (Fig. 4M) with lateral constrictions; posterior lobes separated by very broad median cleft; terminal margins of left and right lobes round, with short setae mesially.

Variations.—A marked sexual dimorphism is seen in chelipeds. Right cheliped of female (Fig. 3H–L) distinctly more slender and more compressed dorsoventrally than male; dactyl shorter than palm, 0.48:1.00, cutting edge with 2 broad but weak calcareous teeth on proximal half and many small corneous teeth on distal half; fixed finger not forming hiatus with dactyl, cutting edge with minute calcareous teeth on distal half; palm long, with dorsal face flat and weakly granular; carpus long and slender, approximately equaling palm in length, dorsal surface flat, with dorsolateral and dorsomesial margins each forming distinct ridge bearing row of large tubercles; merus with row of large tubercles and long setae on dorsal margin, dorsodistal angle bearing strong spine, ventromesial and ventrolateral distal angles each with blunt-tipped spine. Left cheliped of female (Fig. 2M–P) more slender than male; slightly shorter than right, 0.90:1.00; more slender than right, 0.75:1.00 in widest portion of palm and 0.79:1.00 in widest portion of carpus; dactyl and fixed finger straight, not forming hiatus; palm slender, with dorsal surface minutely tuberculate, median portion flat; carpus longer than palm, 1.46:1.00, slender, dorsal surface flat, dorsolateral and dorsomesial margins forming ridges, each bearing distinct row of granules; merus with dorsal face tuberculate, dorsodistal an-

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(mesial view); O, carpus and distal portion of merus (lateral view); P–R, third pereopod (left): P, whole (lateral view); Q proximal portion of carpus and distal portion of merus (lateral view); R, merus (mesial view). Scales = 1 mm.

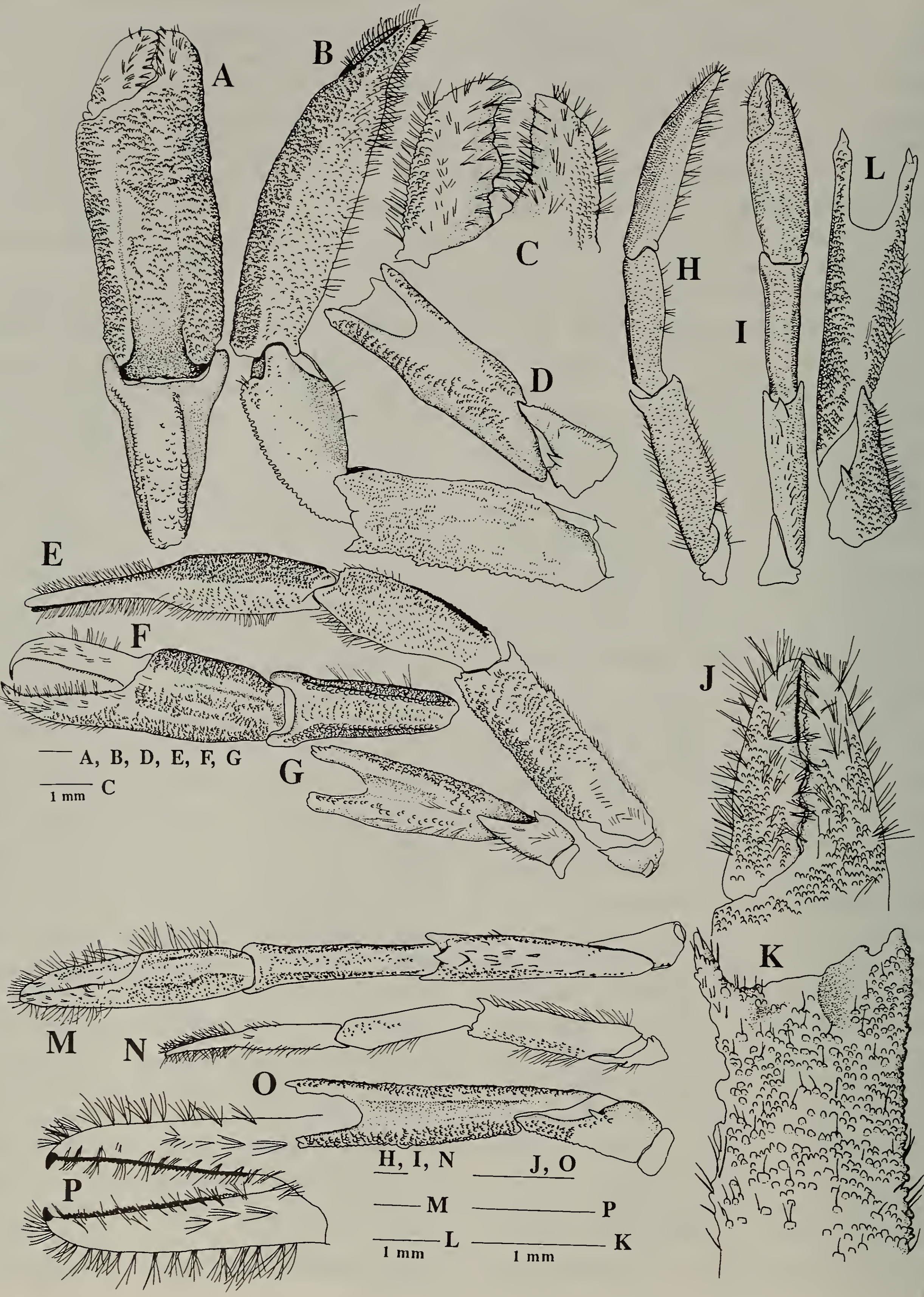

Fig. 3. *Icelopagurus tuberculosus*, new species. A–D, male right cheliped: A, whole (dorsal view); B, whole (lateral view); C, dactyl and fixed finger (dorsal view); D, merus and ischium (ventral view); E–G, male left cheliped: E, whole (lateral view); F, whole (dorsal view); G, merus and ischium (ventral view); H–L, female right cheliped: H, whole (lateral view); I, whole (dorsal view); J, dactyl and fixed finger (dorsal view); K, distal portion of merus (lateral view); L, merus and ischium (ventral view); M–P, female left cheliped: M, whole (dorsal view); N, whole (lateral view); O, merus and ischium (ventral view); P, dactyl and fixed finger (ventral

gle bearing very large spine, with distal angles each bearing blunt-tipped spine.

The size of the abdomen is subject to variation. The abdomen is small in the holotype male and comparatively reduced in male and female paratypes, although no distinct morphological variations are seen in the uropods and telson. Neither the number or shape of the pleopods differ between the holotype and paratype males.

Coloration.—Unknown.

Habitat.—10–20 m, sandy bottom. Housing unknown.

Distribution.—Known only from the type locality, Kumejima, Okinawa.

Etymology.—The name *tuberculosus* is from the Latin, *tuberculum*, diminutive of *tuber*, a swelling or lump, and the suffix, *-osus*, alluding to the tuberculate surfaces of the shield and pereopods characteristics of this new species.

Remarks.—Because the posterior portion of the abdomen of the paratype female is damaged, it cannot be confirmed whether or not it had a fourth pleopod.

Comparison with Icelopagurus crosnieri—The new species agrees with all of the diagnostic characters of *Icelopagurus* proposed by McLaughlin (1997) but is unique in having a large well-calcified, immovable plate that is partially fused with the posterior and posterolateral margins of the shield. This plate is most probably derived from the right and left accessory portions of the shield (sensu Lemaitre 1995) plus the linea transversalis (sensu Boas 1926, Pilgrim 1973). Generally in hermit crabs (excluding Pylochelidae and Lithodidae), the accessory portions of the shield consists of small, elongated movable, partially-calcified plates on either side of the posterolateral margin of the shield. The linea transversalis is a narrow, uncalcified hinge separating the gastric and cardiac regions of the carapace. However, as discussed below, well-developed and strongly-calcified accessory portions and linea transversalis occur in five genera which comprise a highly specialized group within pagurids (Poupin & McLaughlin 1996, McLaughlin 1997).

McLaughlin (1997) did not mention accessory portions of shield and linea transversalis in *Icelopagurus crosnieri*. Two paratype specimens of that species were examined (Fig. 1I, J, N), and no such structures were found; instead, there is a pair of broad, partially-calcified accessory portions of the shield and a narrow, uncalcified linea transversalis along the posterior margin of the shield. These structures are clearly separated from the shield by a soft membrane (Fig. 1I, J).

The morphology of the dorsal surface of the shield in the new species, *I. tuberculosus*, is also distinct. Anteriorly there is a transverse row of four prominent protuberances and a pair of similar protuberances on the anterolateral margins, all strongly armed with minute tubercles. The ocular peduncles are also distinct, armed with many tubercles. None of these characters occur in *I. crosnieri*.

The size of the abdomen of *I. tuberculosus* is small or somewhat reduced (Fig. 1K–M). The abdomen in *I. crosnieri* is normal, similar to that of typical pagurid crabs (Fig. 1N). Other morphological differences between the two species are given in Table 1.

Discussion

When establishing *Icelopagurus*, McLaughlin (1997) stated that it was superficially very similar to *Catapagurus*, both genera being characterized by a well-developed right sexual tube in males, females lacking specialized secondary sexual char-

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view). A–G, holotype male, SL = 5.70 mm, Okinawa, Japan (CBM ZC 4700); H–P, paratype female (CBM ZC 4702), SL = 5.10 mm, Okinawa, Japan. Scales = 1 mm.

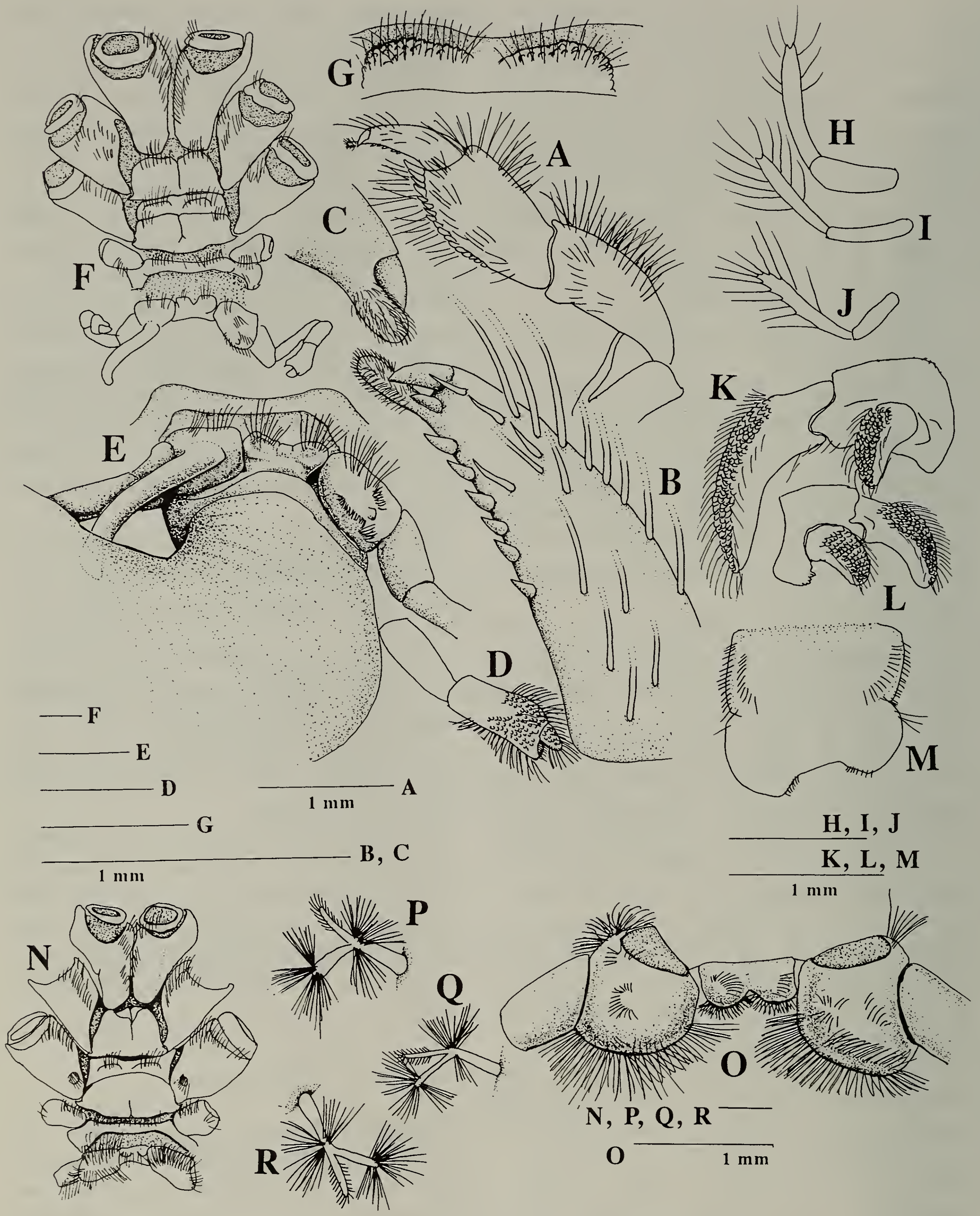

Fig. 4. *Icelopagurus tuberculosus*, new species. A–C, fourth pereopod (left): A, whole (lateral view); B, dactyl (lateral view); C, terminal claw and preungual process of dactyl (mesial view); D, fifth pereopod (right); E, coxae and sternite of fifth pereopods of male (ventro-posterior view); F, coxae and sternites of second to fifth pereopods of male (ventral view); G, anterior plate of sternite of third pereopods (ventral view); H–J, first to third pleopods of male (arising from third to fifth abdominal somites); K, left uropod; L, right uropod; M, telson (dorsal view); N, coxae and sternites of second to fifth pereopods of female (ventral view); O, coxae and sternite of fifth pereopods of female (ventral view); P–R, first to third pleopods of female (arising from second to fourth abdominal somites). A-M, holotype male, SL = 5.70 mm, Okinawa, Japan (CBM ZC 4700); N–R, paratype female, SL = 5.10 mm, Okinawa, Japan (CBM ZC 4702). Scales = 1 mm.

Table 1.—Comparison of morphology of ambulatory pereopods and telson in species of *Icelopagurus*.

	I. tuberculosus, new species	*I. crosnieri*
Second and third pereopods		
Dactyl: mesial face	concave	flat or slightly convex proximally
dorsomesial margin	row of numerous short corneous spines	row of short setae on proximal half and row of every long setae on distal half
ventromesial margin	row of numerous short corneous spines	very few setae
Propodus: dorsal face	granular spine-like setae on distal half	few irregular rows of spines spine-like setae entirely
Carpus: dorsal face	granular	few irregular rows of spines
Merus: dorsal face	1 or 2 very strong spines	rugose
ventrolateral face	granular	numerous spines
Posterior lobes of telson		
posterolateral margin	unarmed	4 long corneous spine-like setae
mesial margin	unarmed	few calcareous spines

acters, a rudimentary or vestigial external endopodal lobe on the maxillule, more or less reduced crista dentata with one accessory tooth, and a distinct tubular preungual process on the dactyl of the fourth pereopod. However, *Icelopagurus* is readily separated from *Catapagurus* by the shortness of the sexual tube and the distinct development of the telson.

Although the new species, *I. tuberculosus*, differs from both *I. crosnieri* and *Catapagurus* species in having short ocular acicles, the morphology of the ambulatory pereopods of *I. tuberculosis* is more similar to those of *Catapagurus* species which have dactyls shaped like sabre blades, such as *C. granulatus* Edmondson, 1951 and *C. ensifer* Henderson, 1893, than that of *I. crosnieri*. These characters include the ambulatory pereopods ending in sabre blade-shaped dactyls with dorsal and ventral rows of numerous corneous spine-like setae on the mesial face, and the meri having one or two very strong, subdistal dorsal spines. The ambulatory dactyls of *I. crosnieri* are not sabre blade-shaped, their mesial faces having a dorsal row of short setae on the proximal half, very long setae on the distal half, and ventrally only a few setae; the meri of the ambulatory pereopods of *I. crosnieri* lack a distinct dorsal spine.

During the course of this study, similar patterns of calcification were found in the posterior carapace in both *Icelopagurus* and *Catapagurus* species examined (*C. granulatus*, *C. ensifer*, *C. japonicus*, and three undescribed species collected). There are a pair of partially calcified bands in the areas between the cardiac sulci and sulci cardiobranchialis in *I. tuberculosus* (Fig. 1A) and in *I. crosnieri* (Fig. 1I). When McLaughlin & Lemaitre (1997) determined character states of calcification of the posterior carapace of hermit crabs, i.e., entirely calcified; posterolateral and/or posteromedial calcification; and entirely membranous or with only scattered small areas of calcification, they included *Icelopagurus* in the latter category. Although I agree with their classification because of small areas of those partially calcified bands, I think that future detailed studies on patterns of calcification of posterior carapace may provide useful information in hermit crab phylogeny.

McLaughlin (1997) also stated that *Icelopagurus* was ostensibly quite similar to *Pagurodes* Henderson, 1888 sensu stricto, which is currently represented only by *Pagurodes inarmatus* Henderson, 1888. However, *P. inarmatus* differs from both *I. crosnieri* and *I. tuberculosus* in having trichobranchiate gills, fourth pereopod dactyls without a preungual process, and telson with acutely triangular posterior lobes.

The new species, *I. tuberculosus*, shares several characters with taxa considered among the most highly specialized pagurid genera by Poupin & McLaughlin (1996) and McLaughlin (1997), namely, *Alainopagurus* Lemaitre & McLaughlin, 1995, *Alainopaguroides* McLaughlin, 1997, *Solitariopagurus* Türkay, 1986, *Porcellanopagurus* Filhol, 1885, and *Ostraconotus* A. Milne Edwards, 1880. These five genera are characterized by a well-calcified shield, distinct reduction of the abdomen, symmetrical uropods and telson, very broad sternites on the pereopods, absence of paired or unpaired pleopods in males, and lack of left fifth pleopod in females. Because of these morphological similarities, McLaughlin (1997) stated that these genera might conceivably be considered as sister taxa. Since *I. tuberculosus* also has a vaulted, well-calcified shield, a more or less reduced abdomen and elongated, slender chelipeds and ambulatory legs with very broad sternites, general impression of similarity is gained between *I. tuberculosus* and these genera.

As previously mentioned, the large, well-calcified and immovable plate on the carapace of *I. tuberculosus* is derived from the well-developed and calcified accessory portions of the shield and linea transversalis. The well-calcified condition of the linea transversalis is also seen in the five mentioned specialized genera (Table 2), and in at least two genera, *Solitariopagurus* and *Alainopagurus*, it is partially fused with the shield (Poupin & McLaughlin 1996, Lemaitre & McLaughlin 1995, McLaughlin 1997). The development and strong calcification of shield accessory portions are also known in these genera (Lemaitre & McLaughlin 1995, Poupin & McLaughlin 1996, McLaughlin 1997) (Table 2). In all of these genera, the linea transversalis and accessory portions are not completely fused together, being at best partially fused in *Solitariopagurus* and *Porcellanopagurus*.

In overall morphology, the two species of *Icelopagurus* are quite similar to *Alainopaguroides*, a monotypic genus represented by *A. lemaitrei* McLaughlin, 1997, in the morphology of the shield, cephalic appendages, mouthparts, pereopods and secondary sexual characters in the both sexes (Table 2). *Icelopagurus tuberculosus* is more similar to *Alainopaguroides* than *I. crosnieri* in the short ocular acicles, ambulatory legs with more or less blade-shaped dactyls bearing dorsal and ventral rows of regularly-spaced setae on the mesial face, and a more or less reduced abdomen. *Alainopaguroides* is distinguished from *Icelopagurus* in lacking unpaired or paired pleopods in males, having vestigial propodal rasps on the fourth pereopods, and symmetrical uropods and telson (Table 2). In addition, *I. tuberculosus* differs from *Alainopaguroides* in having large protuberances anteriorly on the shield.

Icelopagurus shares some characters with *Solitariopagurus*, currently recognized as having three representatives, *S. profundus* Türkay, 1986, *S. triprobolus* Poupin & McLaughlin, 1996, and *S. tuerkayi* McLaughlin, 1997. Both genera have a vaulted, well-calcified shield, obsolete or no external endopodal lobe of the maxillule, elongated, slender chelipeds and ambulatory legs, and a moderately long right sexual tube in males. Further characters shared between *I. tuberculosus* and *Solitariopagurus*, but not with *I. crosnieri*, include four large protrusions on the antero-dorsal portion of the shield (except *S. profundus*) with a well-developed, calcified accessory portion (but not fused as one in *Solitariopagurus*), and a more or less reduced abdomen. In *Solitariopagurus*, two or three wing-like expansions (except lateral projections of the shield) occur on each lateral margin of the shield. Also, *I. tuberculosus* has a projection on each anterolateral margin of the shield, and distinct anterolateral angles armed with tubercles. *Solitariopagurus* and *Icelopagurus* are immediately distinguished by a number of gills and shapes of a rostrum, lateral projections, oc-

Table 2.—Comparison of selected morphological characters between *Icelopagurus* and selected, specialized genera.

	Icelopagurus	*Porcellanopagurus*	*Alainopaguroides*	*Alainopagurus*	*Solitariopagurus*	*Ostraconotus*
Gill	11 phyllo.	11 phyllo.	11 phyllo.	11 phyllo.	10 phyllo.	10 phyllo.
Carapace						
Lateral projection development	weak	mod. well	weak	mod. well	mod. well to prominent	prominent
Accessory portion of shield	well calcified[a]/ partially calcified	mod. well calcified, broad[a]	well calcified	partially calcified, triangular[d]	well calcified, quadrate[e]	well calcified[f]
Linea transversalis	well calcified[a]/ uncalcified	partially calcified, broad, small	well calcified, rod-like	well calcified, very broad[a]	well calcified, very broad[a]	well calcified[f]
Ocular acicle	short, simple/ elongate, simple	reduced, simple	short, simple	elongate, multiple	reduced, simple	short, simple
2nd and 3rd pereopod dactyls	blade-shaped/ not blade-shaped	not blade-shaped	slightly blade-shaped	not blade-shaped	not blade-shaped	slightly blade-shaped
Female gonopore	paired	paired	paired	only left	only left	paired
4th pereopods						
Termination	semichelate	semichelate	semichelate	simple	subchelate	subchelate
Preungual process	prominent	absent	prominent	absent	absent	absent
Propodal rasp	1 row	1 row	rudimentary	1 row	1 row	absent
Male sexual tube						
Left	very short[b]	absent	very short	moderately long	short	moderately long
Right	long	absent[c]	long	moderately long	moderately long	moderately long
Abdomen	somewhat reduced /normal	reduced	reduced	reduced	reduced	reduced, folded beneath cephalothorax
Male pleopods	3rd–5th, unpaired left	absent	absent	absent	absent	absent
Female pleopods	2nd–4th?/2nd–5th unpaired, left	2nd–4th unpaired left	2nd–4th unpaired, left	2nd–4th unpaired, left	2nd–4th unpaired, left	2nd–4th, unpaired, left
Uropods	asymmetrical	symmetrical	symmetrical	symmetrical	symmetrical	symmetrical
Telson	asymmetrical	symmetrical	symmetrical	symmetrical	symmetrical	symmetrical
Median cleft	prominent	very small	small	absent	absent	?

In *Icelopagurus*, the character listed first is for *I. tuberculosus*, and the second for *I. crosnieri*. phyllo.: phyllobranchiate gills. a: partially fused with shield. b: a slight protrusion of vas deferens. c: but recently, existence of a protrusion of vas deferens was reported in *P. adelocercus* by McLaughlin & Hogarth (1998). d: described as posterolateral plates of carapace (Lemaitre & McLaughlin 1995). e: described as anterolateral plates of posterior carapace (Poupin & McLaughlin 1996). f: entire carapace is well calcified.

ular facicles and morphology of the abdomen and its appendages (Table 2).

Porcellanopagurus also has two or three wing-like expansions on each lateral margin of the shield (Borradaile 1916, Forest 1951, Takeda 1981, 1985; Suzuki & Takeda 1987, McLaughlin 1997, McLaughlin & Hogarth 1998). However, it differs from *Icelopagurus* in morphology of the abdomen and its appendages, and male sexual tube (Table 2). *Ostraconotus* (based on Türkay 1986, Poupin & McLaughlin 1996, McLaughlin 1997, McLaughlin & Lemaitre 1997) also has the shield with a transverse row of four somewhat large tubercles on the anterodorsal portion, and a right sexual tube in males, but differs from *Icelopagurus* in number of gills and structure of the abdomen and its appendages (Table 2). Furthermore, in the Paguridae, *Ostraconotus* is the only genus in which the posterior carapace is completely calcified (McLaughlin & Lemaitre 1997).

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